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The pollen-tube in some of the Cucurbitaceae *

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(WITH PLATES 16 AND 17)

In a previous paper on the embryology of the Cucurbitaceae¹⁴ it was the writer's intention to deal with the matters suggested in the present title, but lack of evidence on certain points, and other causes, necessitated their omission at that time. It is hoped here to discover some of the controlling factors in the behavior of the pollen-tube in *Melothria*, *Micranpelis* and *Cyclanthera*, one species of each.

The various phases of the development of the pollen-tube have been studied by numerous writers in widely differing subjects, but until recently little has been done to determine the nature of the influence which directs the pollen-tube in its growth. The conclusions, however, based upon anatomical and experimental evidence, have been by no means unanimous, and much still remains to be done in this field of investigation.

The behavior of the pollen-tube has been seen to vary considerably in different groups. The manner in which it approaches the embryo-sac in different cases has led Pirota and Longo²⁷ to recognize three distinct conditions: acrogamy, in which the pollen-tube enters the micropyle, a condition obtaining in the majority of seed plants; basigamy, including those cases in which the tube enters by way of the chalaza, occurring in the Amentiferae; and mesogamy, which thus far has been found in a few cases only and applies to those instances in which the tube enters the nucellus by

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some other route, *i. e.*, traversing the tissues of the funicle and integuments. Such conditions have been observed in *Cucurbita* and *Alchemilla*.²³

In its course from the stigma to the ovule, the pollen-tube may follow a canal through the style where such is available, and intercellular spaces as well, or it may bore through a considerable amount of cellular tissue, which it may or may not affect injuriously. Its course is usually a direct one and the direction of its growth is often influenced mechanically by the structure of the ovary as well as by the distribution of nutritive materials in what has been called conducting-tissue. The influence of the latter as a directing agent has received some attention at the hands of Miyoshi^{20, 21} and others whose work we will discuss more fully later, but the results from various sources go to show that in considering the growth of the pollen-tube we are dealing with problems of chemotropic irritability and the action of stimulating substances whose distribution is indicated largely by anatomical features.

While the pollen-tube in angiosperms is ordinarily devoid of branches, a few cases have been observed in which the tube has divided into a number of branches after having reached the ovule. Hofmeister¹³, describes the branching of the tubes in *Pothos* and *Hippeastrum*, and in the Amentiferae it has been observed in *Corylus*, *Carpinus*³, *Juglans*²⁵, *Hicoria* (*Carya*)⁴, *Quercus*³ and several others. It occurs also in *Cucurbita* as described by Longo¹⁷, and observed by the author. That the branching is associated with the function of absorption has been the accepted view, and the observation of Longo that the branching is in a definite relation to the presence and distribution of starch in adjacent tissues supports this opinion.

Numerous observations have been made on different plants as to the time consumed by the pollen-tube in traversing the distance from the stigma to the embryo-sac. This has been found to vary within wide limits and to be dependent upon no fixed principle except that the immediate approximation of the germ cells is correlated with their degree of maturity. In certain herbaceous plants the time required varies from eighteen hours (*Limnocharis*¹²) to several days (*Crocus*, *Arum*¹³) and even much longer, as in certain

orchids, the difference in time being in no relation to the distance traversed. Among woody plants the time between pollination and fertilization has been observed to vary from one month (*Betula*³), to several months (*Hamamelis*)³⁰, and Conrad⁷ has shown that it is over a year in *Quercus*. It has been shown that in those cases where a longer time is required the pollen-tube passes through a more or less protracted resting period; in these cases also the branching of tubes is more or less common, as appears in *Pinus* and the other cases above cited.

Another phase of the development at this stage which has not received sufficient attention is the effect of the pollen-tube itself on the formation of the fruit, or the effect in some cases of a mere irritation of the stigma. Gaertner¹⁰ reports that with certain plants he was able to obtain sterile fruits as large as normal ones by applying to the stigmas the spores of *Lycopodium*. Tschermak³² reports various cases in the enlargement of the ovary by the use of pollen which did not fertilize the seed. Massart¹⁹ secured partial development of fruits in certain Cucurbitaceous forms by applying triturated pollen to the stigmas. In these cases no seeds were fertilized and it appears that the pollen is the seat of an excitant which penetrates the stigma and determines the survival of the ovary. Furthermore Leclerc du Sablon²⁸ has found that the crossing of melons and cucumbers results in a considerable modification of the quantity and quality of the carbohydrates in the placenta and the pericarp.

The *Cucurbitaceae* have long been under the observation of botanists, and certain features in the development of their fruit have frequently attracted attention. Soon after Amici's discovery of the pollen-tube of *Portulaca oleracea*¹ (1823), Brongniart⁵ (1826) described a cellular conducting tissue in *Cucurbita maxima* Duch. and showed the pollen-tube traversing the beak of the nucellus. He observed that the "spermatic granules" were transported by a canal formed of the intercellular spaces of the tissues of the pistil.

Gaertner,⁹ in 1827, made observations on a number of plants and reported an acid secretion from the stigma in certain cases at the time of maturity, and also a correlation between the amount of pollen on the stigma and the number of seeds produced, and that the number of seeds was increased by cross-fertilization.

Amici,² in 1830, in a letter to Mirbel states that the pollen-tube gradually elongates, descending through the style, and comes into contact with the ovule, each ovule being reached by a separate tube.

Schleiden²⁹ (1844) traced the pollen-tube through the micropyle and point of the nucellus, even to the embryo-sac, in *Pepo*, *Melo*, *Cucumis*, *Lagenaria* and *Momordica*, and in the case of *Momordica* saw the germinal nuclei emerge from the pollen-tube.

Recently Guéguen,¹¹ in his studies on the comparative anatomy of the conducting-tissues of style and stigma, examined, among the *Cucurbitaceae*, *Ecballium Elaterium*, *Cucurbita Pepo* and *Bryonia*. He found the stylar canal present in *Ecballium*, but obliterated in *Cucurbita*, but states that where the stigma is tetramerous the conducting-tissue presents an X-like structure as seen in transverse section of the style. This conducting-tissue he observed extended to the ovules, covering the surface of the placenta. He regards the *Cucurbitaceae* as very uniform in the matter of conducting-tissue.

In 1902 Longo¹⁸ announced that the nutrition of the embryo in *Cucurbita* was performed by means of the pollen-tube. At the base of the neck of the nucellus the pollen-tube expands into a large bulla provided with branches which traverse the nucellus and the inner integument and proceed in intimate relation with the internal layers differentiated from the outer integument. Owing to a cutinization in the walls of the epidermal cells of the nucellus, as well as a suberization in the region of the chalaza, the embryo is soon cut off from the usual source of nutritive materials. The pollen-tube, with its branches rich in plasmatic contents and in starch, and with cellulose walls, furnishes the only points where fluids can enter the nucellus. Thus a haustorial function is ascribed to the pollen-tube, which draws upon the inner layers of the outer integument, itself nourished by the vascular bundles.

In the following year Longo¹⁷ published the results of a more extended investigation, including thirteen genera and several more species. In all the cases examined the branching of the pollen-tube was found as a rule only in *Cucurbita*, though in all cases the course of the pollen-tube was always in accord with the distribution of conducting-tissue. The formation of the bulla at the base of the neck of the nucellus is correlated with the presence of

starch in the same neck. He found no expansion of the pollen-tube when the nucellus contained no starch; it forms simply a bulla without much branching (*Luffa maxima* Hort.) when the starch is normal, in very small grains; it forms a bulla with numerous branches (*Cucurbita*) when the starch is abundant in large grains, often in the form of amylo-dextrine. He concludes further that the course of the pollen-tube is regulated by particular substances which act in a chemotactic fashion; in this conclusion, agreeing with Lloyd.¹⁶ When these substances are developed in the interior of the tissues it (the tube) has an endotropic course; when on the exterior an ectotropic course.

In an earlier article the writer made reference to the behavior of the pollen-tube in some of the *Cucurbitaceae*, and the phenomena observed in certain cases seemed worthy of further investigation. In most cases studied the pollen-tube presented no unusual conditions, but in a few instances the dilation or branching of the tube in the neck of the nucellus was a conspicuous feature. In *Cucurbita Pepo* the facts recorded by Longo were observed, and in other genera was noted a tendency similar, though less marked. The present study deals particularly with three members of the *Cucurbitaceae*, viz.: *Melothria pendula* L., *Micrampelis lobata* (Michx.) Greene, and *Cyclanthera explodens* Naud.

With a view to determining the length of time required for the pollen-tube to traverse the intervening tissue between the stigma and the embryo-sac, recourse was had to the following methods: Buds of the pistillate flowers about to open were covered with small bags of tissue paper tied about the peduncle. This was done usually between 4 and 6 o'clock P.M., and the flowers were usually found open the next morning. The stigmas were then pollinated and the bag replaced. At different intervals of time after pollination the fruits were collected and fixed in separate lots for study. Some were also examined fresh by means of freehand sections. In such preparations the pollen-tubes were easily recognized.

The effects of pollination were apparent soonest in the case of *Melothria*, in which the corolla-lobes close in over the stigma in a few hours. If pollination is not effected the flowers remain open for several days. In *Micrampelis* and *Cyclanthera* the results were

not immediately apparent, only those parts of the stigma upon which the pollen germinated showing any change. Under normal conditions the pistillate flowers of *Melothria* are pollinated early in the morning from staminate flowers which open the same day. The staminate flowers are very ephemeral and fall off usually in a few hours.

The effects of pollination and fertilization in the *Cucurbitaceae* have been carefully studied by Massart,¹⁹ who experimented with *Cucurbita*, *Bryonia*, *Ecballium* and *Thladiantha*. He finds that the excitation which determines the survival and the beginning of the increase in the size of the fruit of *Cucurbita Pepo* is derived from the pollen itself and may be replaced by a traumatism; but that the excitation which provokes the general increase in the fruit proceeds only from fertilized ovules. The placentae, however, do not develop except in the vicinity of the fertilized ovules.

As to the time required for the pollen-tube to reach the embryo-sac, considerable variation was observed, the time varying twenty hours or more, depending on the number and position of the ovules. After twenty-six hours the pollen-tube was observed in the nucellus of *Melothria* and the same condition appeared in *Micrampelis* after nineteen hours from the time of pollination. In *Cyclanthera* no tubes were observed at the ovules until forty-one hours had elapsed. Most of the distance between the stigma and the embryo-sac is traversed by the pollen-tube in three or four hours. During this time the tube has passed through the style and into the ovary. The growth is much slower as the tube nears the micropyle. This feature seems to be correlated with the amount of available reserve food in the tube, which is of course greatest at the beginning of its growth.

In the *Cucurbitaceae* the form and structure of the ovary in different genera varies a good deal, but in most cases the cavity of the ovary is practically filled by the fleshy development of the placentae and the pericarp. A fusion of the ingrowing lobes of the placenta often occurs (*Cucurbita*, *Citrullus*) and leaves no space between them. In a similar way the stylar canal may also be obliterated. In *Melothria*, *Micrampelis* and *Cyclanthera*, however, such fusion does not take place before fertilization. The structure of the ovary in *Melothria* is similar to that of *Cucurbita*, except

that the ovules are arranged in one series instead of several on each flank of the three longitudinally-running placental lobes. Each of the placental lobes is covered with a single layer of cells, abounding in starch and possessed of denser plasmatic contents than those underneath. This layer also lines the narrow stylar canal, and covers the funicles of the ovules.

In *Micrampelis* the structure of the ovary is more complex. Here the normal ovary contains four ovules with their micropyles directed toward the pedicel. These are borne one on each flank of the two inwardly-growing placental lobes. In this case, however, the placental ridges become partially fused and grow downward toward the base of the ovary. In this genus as in *Melothria*, the cells which line the stylar canal and cover the placental lobes are filled with starch and denser protoplasm. Starch is also found in the underlying cells to a greater degree than in *Melothria*, but it is most abundant near the stylar canal and ovarian cavity.

Cyclanthera presents a condition in which there is one placental ridge in the ovary with a row of ovules on each flank. Here too the covering of the placenta and the lining of the stylar canal is similar to that of *Melothria* and *Micrampelis*. Both the epidermal covering of the placenta and that of the ovary-wall lying opposite (FIG. 14) are alike filled with starch, but those on the placenta are larger and more columnar in character. Here to a greater degree than occurs in the other cases the tissue beneath the epidermis is supplied with starch. Quite different from this is the condition found in *Cucurbita Pepo*, in which the conducting-tissue is devoid of starch. In *Cucurbita* the conducting-tissue consists of several layers of cells formed by the periclinal division of the epidermal cells covering the placentae.

The course of the pollen-tube in all cases under consideration is along the conducting-tissue just described. In *Melothria*, *Micrampelis* and *Cyclanthera* the tubes proceed down through the stylar canal and over the surface of the placentae. The tubes proceed upon the surface of the lobes wherever possible and not through them as a rule. In the restricted space of the style, where the canal offers insufficient space to accommodate many tubes, they traverse the surrounding tissues and break them down to a considerable extent. In such conditions, and elsewhere, where the

course of the tube lies through the tissues, it appears to travel through the intercellular spaces. The destruction of cells in its path seems to be due mostly to mechanical action and not to digestive enzymes, except in the nucellus of *Cyclanthera*. Fresh ovaries when teased apart showed the pollen-tubes in the stylar canal and passing over various parts of the placental surface. FIGURES 1 and 3-5 represent the course of the tube.

When the surfaces of the placentae are pressed together or against the ovary-wall, the space through which the tubes move is considerably restricted. Under such circumstances they crowd aside the cells of the conducting tissue (FIG. 11). Sometimes a tube may be seen to have passed under the conducting layer (FIG. 15). Where the tubes traverse the ovarian space in *Melothria* they sometimes develop transverse walls or plugs. The manner of their development appears to be the formation of a ring transversely which gradually narrows the aperture until it is completely closed. An excessive development in thickness of this wall sometimes follows, forming plugs as shown in FIGURE 2 *a, b, c*. Similar plugs have already been observed by Osterwalder²⁶ in *Aconitum Napellus*, and by others.

The pollen-tube proceeds by an approximately direct course to the micropyle, and passes down through the nucellus to the embryo-sac. In the apex of the nucellus it usually expands to several times its normal diameter in *Cyclanthera* (FIGS. 6, 13), and from this point sends down a straight and narrow tube to the embryo-sac. Sometimes the entire neck of the nucellus is destroyed by the dilation of the tube. This expansion of the pollen-tube in the apex of the nucellus occurs frequently in *Melothria*, though it was never observed to reach the same proportions as in *Cyclanthera*. In *Micrampelis* also such conditions were sometimes observed; here, however, they are not the rule but the exception. In such cases, both in *Melothria* and *Cyclanthera*, the contiguous cells were destroyed.

That such dilations of the pollen-tube are directly correlated with the occurrence of starch in the surrounding tissues is maintained by Longo, as above pointed out; but the behavior of the pollen-tube of *Elodea*, as described by Wylie,³³ indicates that such conditions are not always the cause of the enlargements of the tube,

for in this case they occur in the ovarian cavity. This has already been suggested by Lloyd¹⁶ in discussing the pollen-tube in the *Cucurbitaceae* and *Rubiaceae*.

In the plants here under consideration the nucellus is practically devoid of starch, which is abundant in the integuments of *Micrampelis* and *Cyclanthera*, though not so abundant in *Melothria*.

The anatomical character of the conducting-tissue is a feature of some interest. In all cases examined a continuous conducting-tissue reaches from the stigma to the micropyle. In *Micrampelis* the neck of the nucellus pushes through the micropyle, and comes out even with the top of the integuments. Practically the same conditions exist in *Cyclanthera*, but in *Melothria* the apex of the nucellus is usually overtopped by the integuments. In the three genera just mentioned the conducting-tissue consists of a single layer of cells, the epidermis covering the placenta and lining the stylar canal. This layer appears to be the only one serving directly as conducting-tissue. On the stigma the starch is restricted to the subepidermal tissue, none appearing in the more densely plasmatic cells of the epidermis. The glandular character of the epidermal cells is quite apparent both on the stigma and in the interior (FIGS. 9, 11, 14). In the interior the cells in the path of the pollen-tubes show indications of activity, by the dense aggregation of the cytoplasm next the exposed side and surrounding large and conspicuous nuclei.

Considerable effort has been made to determine the directive force controlling the movements of the pollen-tube. We may note in passing that Nawaschin,²⁴ Zinger³⁴ and some others have interpreted the endotropic and ectotropic behavior of pollen-tubes as of phylogenetic significance. But evidence at present available seems to point to physiological processes and mechanical relations as the determining factors. In favor of this view we may cite the anatomical evidence contributed by Lloyd¹⁵ in the *Rubiaceae*, Longo¹⁷ on the *Cucurbitaceae*, and the observations of Capus⁶ and of Guéguen,¹¹ and the results of the experimental studies of Miyoshi^{20, 21} and others. Molisch²² has shown that pollen-tubes are positively chemotropic and some negatively aerotropic. Miyoshi sowed pollen-grains on agar in which were imbedded pieces of stigma, ovary, and ovules of different degrees of development. The pollen-tubes

grew toward the pieces from the vicinity of the stigma and were most strongly attracted by ovules ready for fertilization, growing into the micropyle in each case. He concludes that this stimulant is in the nature of a fluid, and in another article has shown that pollen-tubes grow into the stomata of *Tradescantia* leaves, the intercellular spaces of which have been filled with sugar solution. That the pollen-tube is also directed mechanically in its course is maintained by Miyoshi, and Capus states that the mechanical rôle of the conducting-tissue consists in placing the pollen-tube in relation with the micropyle, and that its economy and simplicity depend on the structure of the ovary.

That the stimulants which direct the pollen-tube are nutritive in character is quite evident. Dalmer⁸ states that pollen-tubes are nourished by amyloid substances secreted by stigma, stylar canal, and the interior of the ovary, though he maintains that the entrance of the pollen-tube into the ovule is a purely mechanical phenomenon. Miyoshi points out that sugar as a stimulant can operate only extra-cellularly, and it is plain that where the course of the pollen-tube is intercellular or through the locular space of the ovary that its growth must be at the expense either of the reserve materials within the tube or of substances elaborated by the tissues in its path. The cytological features of the conducting-tissues of the *Cucurbitaceae* here under consideration are similar to those of certain nectaries in the abundance of starch and quantity of cytoplasm, appearance of molecular structures, etc. The evidence here points to the secretion of carbohydrates (probably sugar) as the nutritive material. That the pollen-tubes are partial to the more glandular cells is indicated in *Cyclanthera*. In this case the ovary sometimes shows a considerable locular space at the time of the entrance of the pollen-tubes. The epidermal cells of the placenta are larger and more glandular in appearance than those of the ovary-wall opposite. Though their distance apart is not great, the pollen-tubes always cling to the placenta instead of to the opposite wall, though that likewise is supplied with starch.

One noticeable feature of the relation between pollen-tube and conducting-tissue in *Melothria*, *Micrampelis* and *Cyclanthera* is the fact that while starch is abundant in the conducting-tissue, none appears in the tube. In *Cucurbita Pepo* on the other hand the condi-

tions are reversed, and starch is entirely absent from the ample conducting-tissue, though abundant in the pollen-tube almost to the time of its entrance into the embryo-sac. These facts are regarded as evidence that the directive stimulant, in these cases at least, is of a different character from the substances in the tube. It is, however, recognized that the absence of starch from the cells of the conducting-tissue may not mean an absence of soluble carbohydrates, for no starch is visible in the secreting cells of some nectaries. The application of iodine to sections of the style and ovary of *Cucurbita* easily brings out the pollen-tubes in contrast with the conducting-tissue, the former rich in starch, coloring a dark blue, the latter a deep yellow, indicating an abundance of albuminous material. The pollen-tube branches in the nucellus according to the disposition of starch, as above cited in reference to Longo's work.

If the growth of the pollen-tube or its branches is thus regulated by the occurrence or distribution of nutritive material, we have apparently an explanation for the growth of the tube through the nucellus to the embryo-sac, structures which, in the cases here considered, are normally filled with starch before the approach of the pollen-tube.

At what distance from the ovule the pollen-tube comes under its influence, has not in these cases been determined, but it is evident that the embryo-sac is the source of a stimulant of some sort by which the pollen-tube is directed unerringly toward it. As to the character of this stimulant the evidence is meager, but what there is seems to indicate a sugar.

Miyoshi's results with the pollen of *Digitalis* and numerous other plants show that their tubes are sensitive to the presence of certain soluble carbohydrates, but are indifferent to or repelled by a variety of other substances. Moreover, the fact cited elsewhere by the same author to the effect that the pollen-tubes of distantly related plants were attracted to the same ovule and to different ovules would indicate that the stimulant is some substance quite common in plant tissues.

It is suggested here that a difference in the degree of concentration of such a solution as a sugar may be a sufficient factor in directing the pollen-tube. This is in accord with the observations of Miyoshi and others.

As to the particular organ of the embryo-sac responsible for the discharge of the stimulant, opinions have differed, some ascribing that function to the synergids and others to the egg-cell (Strasburger³¹, Lloyd¹⁵). But to the writer it seems more probable that the source of such a stimulant may be found in the endosperm-nucleus and its cytoplasm. The appearance of this nucleus, indicating the large degree of activity, and its abundant cytoplasm filled with starch would favor such a view. The pollen-tube is presumably ruptured upon entering the embryo-sac by the rapid absorption of water and consequent increased turgor, and its contents discharged into the male generative nuclei come under the influence of the egg-cell and fertilization takes place, and in some cases also the fusion with the endosperm-nucleus.

SUMMARY AND CONCLUSIONS

1. The behavior of the pollen-tube was studied in *Melothria pendula*, *Micrampelis lobata*, and *Cyclanthera explodens*. As observed in these cases the time elapsing between pollination and the arrival of the pollen-tube at the embryo-sac was twenty-six hours in *Melothria*, nineteen hours in *Micrampelis*, and in *Cyclanthera* forty-one.

2. The pollen-tube follows conducting-tissue which for the most part is formed of the epidermis lining the stylar canal and covering the placental lobes. The tube traverses this tissue by passing over its surface wherever possible, and rarely affects the cells injuriously. The conducting-tissue of these plants is abundantly supplied with starch. In *Cucurbita Pepo* starch is wanting in the conducting-tissue but present in abundance in the pollen-tube. In all cases observed where starch abounded in the conducting-tissue it was absent from the pollen-tube. The pollen-tube appears to be directed by nutritive substances secreted by the conducting-tissue. Attention is called to the similarity in anatomical features of the cells of the conducting-tissue to those of certain nectaries, as evidence as to the nature of the secretion.

3. It is thought that the pollen-tube comes under the influence of a stronger stimulant emanating from the ovule. It is suggested that the source of this stimulus may be the endosperm-nucleus.

4. The evidence at hand supports the contention of Miyoshi and others that the behavior of the pollen-tube is a phenomenon

of chemotropism as against its being due to mechanical conditions or of phylogenetic significance.

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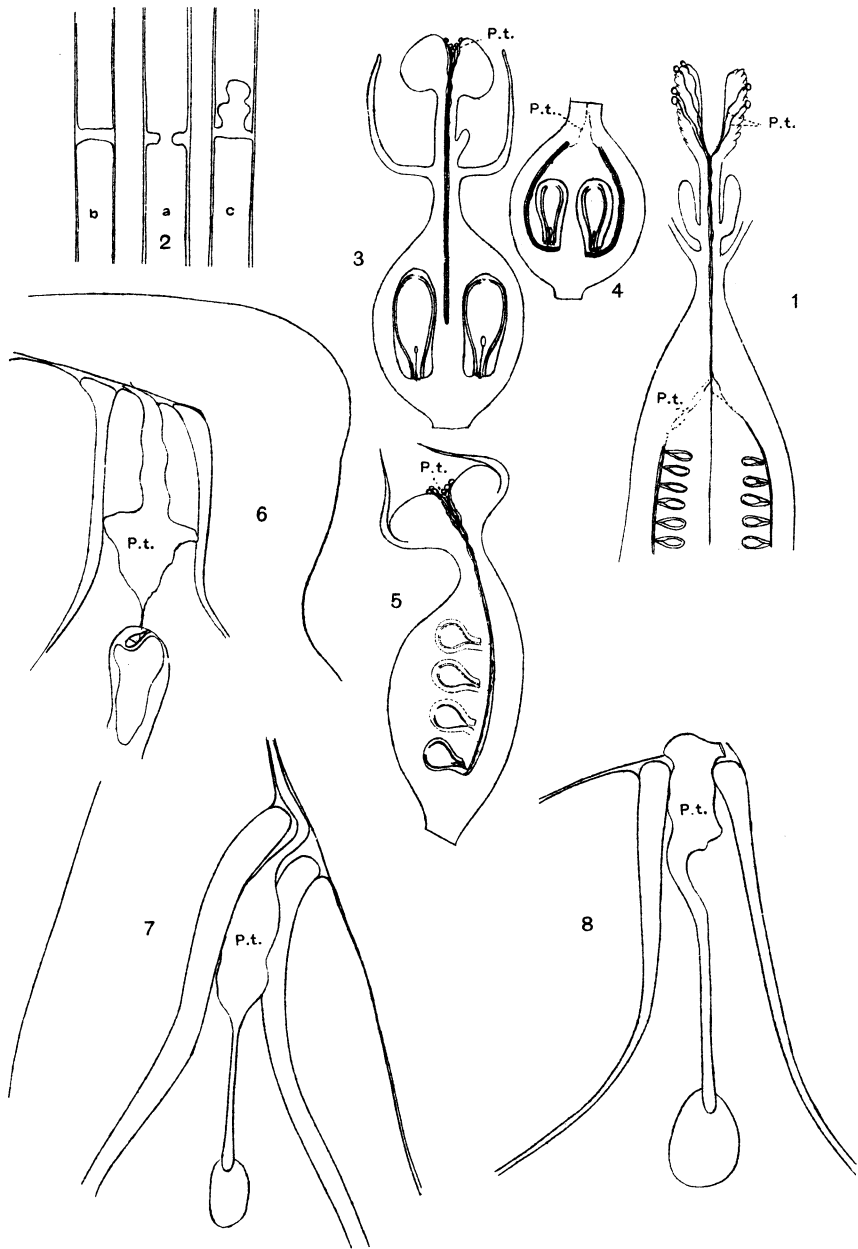
Description of plates 16 and 17

PLATE 16

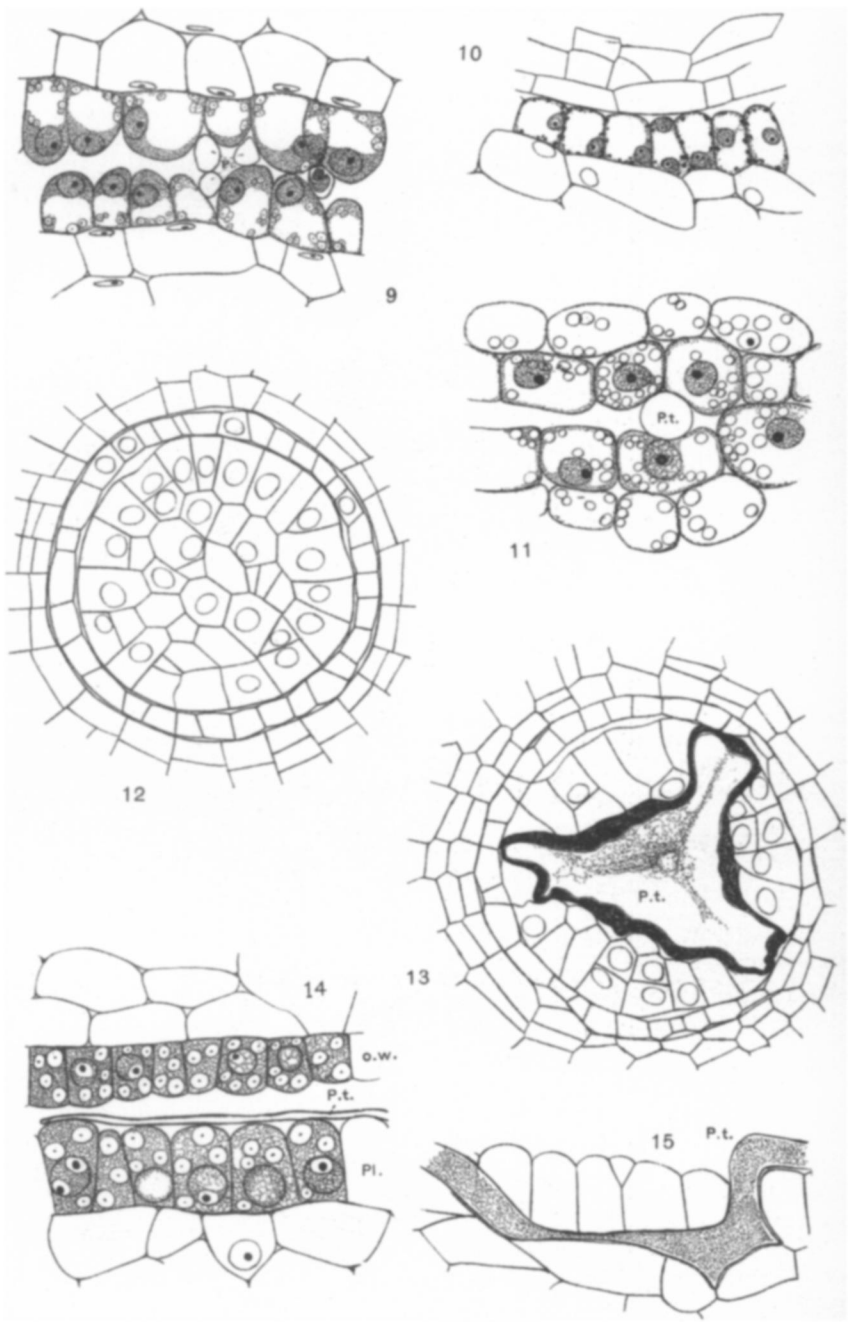
1. Diagrammatic figure representing longitudinal section through gynoecium of *Melothria*. Course of pollen-tube (*P. t.*) intercellular.
2. *a, b, c.* Pollen-tube showing plugs.
3. Longitudinal section through gynoecium of *Micranthelia*. Conducting-tissue shaded.
4. Ovary of same at right angles to figure 3.
5. Longitudinal section through ovary of *Cyclanthera*, showing path of pollen-tubes.
6. Diagram of micropylar region of ovule of *Cyclanthera*, showing dilation of pollen-tube, *P. t.*
7. Ditto, *Melothria*.
8. Ditto, *Micranthelia*.

PLATE 17

9. Conducting-tissue of *Melothria* on placental folds. Pollen-tube in transverse section. $\times 440$.
10. Conducting-tissue on funicle of ovule of *Melothria*. $\times 440$.
11. Conducting-tissue of *Micranthelia*. Transverse section of pollen-tube. $\times 440$.
- 12, 13. Transverse section through neck of nucellus, in *Cyclanthera*, before and after passage of pollen-tube, *P. t.* $\times 440$.
14. Conducting-tissue in ovary of *Cyclanthera*. *Pl.*, placenta; *o. w.*, ovary-wall; *P. t.*, part of pollen-tube. $\times 440$.
15. Same showing pollen-tube (*P. t.*) passing under some cells of conducting-tissue. $\times 440$.



1,2,7. MELOTHRIA. 3,4,8. MICRAMPELIS. 5,6. CYCLANTHERA



9,10. MELOTHRIA. 11. MICRAMPELIS. 12-15. CYCLANTHERA